CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS[1]

VI. Certain Filicinean Fructifications

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Carboniferous plants collected from the roof shales of American coal mines received comprehensive treatment at the hands of paleobotanists of a half century ago, the better known and basic contributions being those of Lesquereux ('80-'84) and White ('99). However, in view of our increased knowledge of the floras that these men dealt with, as well as the recent innovations in the technique of handling compression fossils, extensive revisions in the literature are necessary. Furthermore, modern methods now render very valuable the comparatively small, scattered, and fragmentary specimens of fertile fronds that apparently had been discarded in favor of the larger and more attractive museum-type of specimen. In most cases these were sterile and in themselves of little biological value.

During the past year I have obtained, largely through the kind offices of Mr. John Jones, Safety Superintendent of the Old Ben Mines, in Franklin County, Illinois, a number of interesting specimens bearing filicinean fructifications. The specimens are not numerous, and generally only small portions of the entire frond are present. They do, however, display characters pertaining to the morphology of spores and sporangia, characters that are considered to be of prime importance in the diagnosis of living forms. Although our investigations thus far must be considered as only an introduction to more extensive and critical studies, it seems advisable to present the results to date in view of current war-time regulations which prevent further collecting in the shaft mines.

All of the specimens described in the following pages were obtained from the roof shales of the Old Ben Mine No. 11. These shales overlie coal No. 6 and constitute the basal member of the McLeansboro formation (upper Allegheny), being of upper-middle Pennsylvanian age.

SCHIZAEACEAE

Senftenbergia Corda. 1867.

This genus has come into prominence recently by Radforth's ('38-'39) demonstrations that *Dactylotheca* Zeiller is founded on a misconception and that forms previously assigned to it must be referred to *Senftenbergia* or *Asterotheca* (Radforth, '42). Furthermore, it has been shown that *Senftenbergia*, so far as its critical characters are concerned, belongs emphatically in the Schizaeaceae. Specimens of the type that Kidston believed referable to *Dactylotheca* have long been

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known in America, but modern technique has now confirmed Radforth's conclusions from American material in striking fashion. The material studied was obtained in association with fronds of *Pecopteris plumosa* var. *dentata,* discussed below, and strongly suggests that the characters exemplified by the *Senftenbergia* pinnae are correlative with these sterile fronds.

Technique.—

The technique employed was essentially the same as that described by Radforth in the above-cited papers, and by Andrews and Pearsall ('41) for carbonaceous compressions of a Cretaceous *Anemia.* Only one well-preserved specimen was available, and, in order to obtain sufficient sporangia without affecting the specimen, small portions, about 1 cm. square, were removed with needles, the fossil side coated with a nitrocellulose solution and immersed in dilute hydrofluoric acid overnight (very small fragments were placed in the acid directly). When the shale-free sporangia were then placed in the oxidizing fluid (nitric acid and potassium chlorate), followed by washing in dilute ammonia water, their walls gradually cleared, revealing the contained spores. Three to four hours were sufficient, in most cases, to bring about the almost complete disintegration of the sporangium wall, isolating the spores as a unit mass (figs. 7, 8). The material thus prepared was mounted in "crystal white" Karo.

Senftenbergia plumosa (Artis) Radforth var. **Jonesi** Andrews, n. var.

Judging from the two pinnae composing the specimen (fig. 1) they are parts of a comparatively large frond, and the size attained by the supposed sterile frond (or portion thereof) supports this assumption. Almost the entire under-surface of the secondary pinnae appears densely clothed with sporangia (figs. 2, 3) which are attached by a short stalk (figs. 4, 5). The mature ones that have shed their spores exhibit but little variation in size, averaging .52 x .26 mm. The annulus is distinctly Schizaeaceous, consisting of a nearly apical ring of two rows of longitudinally elongate and irregularly interlocking cells (figs. 5, 17). It is difficult to locate specimens which display the apical plate in end view, since the great majority of the sporangia have been laterally compressed in fossilization. Figure 16 shows the distal end of a sporangium, from which it seems clear that the apical plate consists of a number of cells, comparing closely with the apical plate of living *Anemia* species.

Many of the sporangia still retain their spores. The less mature spores are smooth-walled and adhere together tenaciously in a more or less ovoid mass, although tapering somewhat toward the proximal end (fig. 8). The mature spores (fig. 9) are approximately 50 μ in diameter and are characterized by irregular ridges and stout spines which may be forked at their tips.

During the course of treatment in the oxidizing fluid one sporangium was observed in which the spores were almost mature judging from their sculpturing, yet still retained together in a unit mass after dissolving the sporangium wall. Most of the spores were readily separated with a needle, and the number determined was approximately 118. That the spore mass represents the entire contents of a sporangium was evinced by its uniform shape conforming to that of the sporangium as a whole prior to treatment.

It is not possible to discern distinctly a lamina in the fertile pinnae but that such was present seems evident from the abundance of epidermal hairs that clothe not only the pinna rachis (fig. 15) but the secondary pinnae as well. The hairs and sporangia cover a sufficiently wide area as to leave no reasonable doubt that a lamina was present although it may have been somewhat narrower than the sterile foliage.

The hairs vary somewhat in size, are branched (figs. 6, 17), and display irregularly thickened cross-walls. The technique involved in handling such delicate structures was necessarily specialized and is perhaps worth a separate notation. A portion of the specimen was dipped in 20 per cent hydrofluoric acid for about one minute. This cleared the dark gray shale to a much lighter shade and tended not only to partially liberate the sporangia and hairs from the matrix but, due to the increased color contrast, greatly enhanced study and photography. Hairs were then carefully removed with needles and placed in the oxidizing fluid for about three minutes. After washing and treatment with ammonia water the larger branched ones appear as shown in fig. 17. If the oxidation time is prolonged the hairs become nearly colorless and so fragile as to be exceedingly difficult to manipulate.

Discussion.—

Of the European species of *Senftenbergia* described by Radforth our specimen agrees very closely with *S. plumosa.* The general appearance of the sporangia and their contents is almost identical in the two and they compare very closely in size as shown in table I.

TABLE I

A DIMENSIONAL COMPARISON OF THE SPORANGIA AND SPORES OF *S. PLUMOSA* AND *S. PLUMOSA* VAR. *JONESI*

	Sporangium length (mm.)	Sporangium width (mm.)	Spores per sporangium	Spore diameter (μ)
Senftenbergia plumosa (Artis) Radforth	.54	.27	200	50
S. plumosa (Artis) Rad. var. *Jonesi*	.52	.26	118	50

It may be seen that there is no appreciable difference in sporangium or spore size although a discrepancy appears in the reported number of spores per sporangium. I am inclined to believe that Radforth's number, which is based on calculation, is high in view of the fact that the one given here is based on an actual count and the spores and sporangia of both agree very closely in size. The structure of the annulus and spore exine sculpturing also compare very closely (cf. Radforth, '38, pl. II, fig. 6). Radforth's figures do, however, seem to display a more prominent lamina than the Illinois specimen, although this may be due simply to poorer preservation in the latter. Because of that difference, as well as the variation in reported spore output and certain variable characters relating to the suppósed sterile foliage, it seems advisable to designate the specimen described here as a distinct taxonomic entity.

STERILE MATERIAL

Pecopteris plumosa var. **dentata** (Bgt.) White.

We have found associated with the above-described fertile material numerous specimens of a Pecopterid-type frond. In view of our knowledge of the foliage of other species of *Senftenbergia,* as well as certain characters exemplified by S. *plumosa* var. *Jonesi* which are correlative with this particular *Pecopteris,* this will be considered in some detail.

This plant and its close relatives have been described many times and there is little occasion to repeat the descriptions. Although the outline of the large fronds may have been lance-shaped, it nevertheless seems inappropriate to describe a highly pinnatifid leaf of this sort as "lanceolate." Part of Kidston's ('24, p. 385) description of fronds which he referred to *Dactylotheca plumosa* applies very well to our specimens. "The pinnules on the middle ultimate pinnae are oval-triangular or broadly lanceolate (in general outline) with rounded apices, and united by the whole width of their base to the rachis. The basal inferior pinnule is deltoid-rounded, generally smaller than the others, and occupies the angle formed by the insertion of the pinna on its parent rachis, and frequently has a distinct lobe; the superior basal pinnule is oval or oval-oblong, obtuse, and is almost invariably the largest pinnule on the pinna. The uppermost pinnules become gradually more united to each other and form a more or less lobed, and finally an entire blunt apex to the pinna." Bell ('38, p. 76) also mentions "the punctate rachides of primary pinnae," . . . "the contiguous, smooth-surfaced pinnules which have convex, upper surfaces and a tongue-shaped or subtriangular form. The apparently pointed apices of the pinnules in some specimens have resulted from inrolling of the margins, . . ." This last feature is particularly noted in transfer preparations of the Old Ben material; the infolding may ostensibly shorten the distal inferior pinnule margins in unprepared material by more than half a millimeter and serve to give them a notably triangular aspect so that some of the pinnae appear rather sharply serrate as shown in fig. 13. The venation and form of the basal pinnules are shown in text-fig. 1.

The specimens at hand are notably larger than those described from the Barnsley horizon. The one illustrated in fig. 14, at reduced size, is the most delicate yet seen in the Old Ben material, and it appears significantly more robust than Kidston's Yorkian forms. In a recent collection we obtained a particularly fine and large frond fragment. Judging from the size of the primary pinnae, the

Text-fig. 1. Venation and shape of superior and inferior basal pinnules of *Pecopteris plumosa* var. *dentata*. x 5.

longest of which measures 37 cm., it is safe to say that the frond attained a length of between 1 and 2 meters.

Nearly all of our material is well preserved as coalified compressions. All the veins are sunken on the upper surface which is almost invariably exposed. When portions of the upper side of the lamina do remain attached to the rock the counterpart is apt to still carry a skeleton of the veins distinctly impressed. Thus the veins of pinnules are shallow grooves in the upper surface and prominences of the lower surface. The primary and secondary rachides show a number of irregularly spaced papillose protuberances which no doubt represent enlarged and sclerified hair bases. These are on both upper and lower surfaces of the primary rachis but seem more limited to the lower surface of the secondary branches; the tertiary rachides do not show them clearly, partly because the basal pinnules overlap the rachis (cf. text-fig. 1) and probably also because the emergences on this part of the frond are more delicate. On the secondary rachides the hairs are by no means as numerous as shown by Radforth ('38, p. 1, fig. 1) on a Barnsley specimen.

Cuticular preparations have been made from median pinnae similar to those shown in fig. 13, and from this same specimen. The structure varies dorsally and ventrally and in relation to the veins. Over the veins on the upper surface the cuticle is thin and in maceration frequently splits apart along them. The fragment shown in fig. 11 represents the upper cuticle between the bifurcate tips of one of the lateral veins. Although the central cells tend to be isodiametric, pentagonal or hexagonal, many are elongated. The largest are about 40 x 70 μ in diameter; more isodiametric cells measure about 35 μ. The central elongate cells show no special orientation but toward the veins their long axes parallel the nervation and over the veinlets the cells are still narrower. Due to the delicacy of the cuticle these cell markings are shown indistinctly. Other cuticular fragments show that the veins extend to the margin of the lamina which may be very slightly indented. The cuticle is thicker at the margin, tending to show very elongate rugose markings as may be seen in fig. 10, which represents the ventral and dorsal cuticles connected at the leaf margin and spread out in a single plane. The lower cuticle is much thinner than that covering the upper surface. The cells are elongate, roughly rectangular, and tend obliquely from the margin as shown in figs. 10 and 12. The largest cells are about 30 x 80 μ, the smallest ones 20 x 40 μ. Triangular cells are seen where the oblique lower pattern merges with that of the margin. Neither stomates nor hairs have been observed on these cuticles. Presumably the stomatal areas are on the lower surface where the cuticle is thinnest and least readily obtained by maceration procedure.

It is difficult to compare these data with those given by Radforth for the sterile fronds he has identified with *Senftenbergia plumosa.* The small cuticular fragment he has figured (pl. 1, fig. 3) shows elongate, truncate-lenticular cells averaging about 45 x 15 μ, and what appears to be a hair base. It seems clear that his specimens are easily distinguishable from those described here. This lends further support for the taxonomic distinction of our material, at least in so far as the sterile specimens are concerned, from the older more delicate Yorkian forms.

The differences between our material, identified as variety *dentata* (Bgt.) White, and that which Kidston and Radforth have shown for the Yorkian *Pecopteris plumosa* may be summarized as follows: in var. *dentata:*

1. Fronds more robust.
2. Rachides more sparsely hirsute.
3. Lower cuticles show a somewhat different type of cell pattern.

MARATTIACEAE

Scolecopteris Zenker. 1837.

This genus is based on elongate, stalked synangia composed of 3–5 exannulate sporangia. Certain workers have expressed the opinion that *Scolecopteris, Asterotheca* and associated genera may be Pteridosperm micro-sporangiate fructifications. I am inclined, however, to accept the more universally prevalent view that they are of Marattiaceous affinities. A more detailed consideration of the taxonomy of the group follows on a later page.

Scolecopteris Radforthii Andrews, n. sp.

Pinnules 1½ times as long as broad; pinnule vein branches once dichotomous; synangia of 3–4 sporangia, in two rows, on vein terminations, near margin of pinnule; spore masses 550 μ long, 165 μ broad; spores 32 μ in diameter, calculated number 900 per sporangium. The species is named for Dr. N. W. Radforth in recognition of his contributions to our knowledge of Carboniferous ferns.

Although this species is based on a small fragment of a frond bearing parts of ten ultimate pinnae the spore-bearing organs are well preserved, and there is no reason to doubt that it is a representative portion of a fertile frond. The sterile foliage is not known. The pinnules are about 1½ times as long as broad and ascending (fig. 20). The vein which passes out from the pinna rachis gives off side branches of which the proximal ones dichotomize once while those near the tip of the pinnule may remain unbranched (fig. 18).

The spore-bearing organs consist of synangia borne in two rows near the margin of the pinnules, each synangium being at the terminus of a vein.

Following oxidation treatment the cleared sporangial walls reveal the spore masses within (figs. 21, 22). Each synangium is composed of 3–4 partially united sporangia. The spore masses themselves are distinct in most cases and average 550 μ long by 165 μ broad. There is some variation, however, in the degree of the union of the sporangia into a synangium. One of the synangia was isolated in which the spore masses were united through the greater part of their length and others have been observed in which the basal part of the spore masses seems to have been fused. These instances are exceptional and perhaps due in part to maceration of the sporangium wall, for in most cases the sporangia tend to become isolated as distinct unit masses of spores.

Dehiscence is by means of a longitudinal slit extending the length of the inner side of the sporangium. The sporangia composing a synangium are apparently rather loosely held together and in most cases split apart at maturity.

The spores, such as those shown in figs. 21, 22 and apparently immature, measure 32 μ in diameter, are smooth-walled, spherical, and display a tri-radiate commissure. A few have been observed bearing slender unbranched spines, but completely mature ones have not been found. According to the method given by Radforth ('39, p. 746), the spore output of each sporangium would be calculated as 1090. The sporangia vary in length from 500 to 700 μ but most are approximately 550 μ. Since these measurements pertain to the isolated spore masses which filled a sporangium and do not include the wall, the size of the whole sporangia would have been appreciably greater. The specimen illustrated in fig. 22 may be taken as a typical example. The fact that the sporangia taper at their distal end would make their total volume somewhat less than that of an ellipsoid (the geometric figure assumed in the above-noted calculation) of the same minor and major axes. Taking this into account an estimate of 900 spores per sporangium may be considered as reasonably accurate. Thus, each synangium produced some 2700 to 3600 spores depending on whether it consisted of three or four sporangia.

The rather crowded nature of the sporangia and the compression that they have undergone make it difficult to portray their organization clearly in a photograph. Consequently, the restorations shown in figs. 23 and 24 have been prepared to present their probable appearance before and after dehiscence in life.

Discussion.—

It becomes increasingly evident that the Marattiaceae, or at least plants bearing Marattiaceous fructifications, were abundant in species as well as numbers of plants in the Carboniferous forests. Of the spore-bearing organs that have been referred to this family the two genera *Scolecopteris* and *Asterotheca* are among the better known, and considerable controversy has arisen as to whether *Scolecopteris* deserves generic rank or whether the species assigned to it should be included within *Asterotheca.*

In his "Handbuch" Hirmer ('27, p. 576) considers *Scolecopteris* as synonymous with *Asterotheca,* and Radforth ('42), in his discussion of *A. parallela,* proffers the same opinion. The present writer feels that this course places entirely too wide a range of spore-bearing structures within a single genus. If one compares typical *Asterotheca* fructifications such as those illustrated by Hirmer (p. 582) for *A. truncata* with species such as Radforth's *A. parallela* ('42, pl. 1, fig. 3), it will be noted that the synangia of the latter appear more or less cylindrical and elongate as compared with the usually flattened disc-like shape of *Asterotheca.*

The macerated synangia of *Scolecopteris Radforthii* (figs. 21, 22) are rather closely comparable with Radforth's figure ('42, pl. 1, fig. 5) of the corresponding structures of *A. parallela;* so similar in fact as to leave little doubt that the two are congeneric. The gross organization of the synangia (figs. 19, 20) is, however, certainly not correlative with *Asterotheca.* The synangia of *A. parallela* and *S. Radforthii* are elongate and stalked, which accounts for their less orderly arrangement in the compressions, especially of the latter. The objection may be raised that the appearance of "typical" *Asterotheca* fructifications is due to compression. It is extremely improbable, however, unless they were naturally short and disc-shaped, that such regularity would result in the fossil state. The restoration of *S. Radforthii* shows the probable appearance of the fertile pinnules in life. Synangia such as these, upon compression, lie more or less flat (longitudinally) against the lamina and so lose in fossilization their characteristic habit. A typical *Asterotheca* presents a radially symmetrical compression indicating a synangium with a comparatively much shorter long axis.

It should be emphasized that I do not in any way criticize Radforth's removal of *A. parallela* from *Dactylotheca* nor his masterly demonstration of the true morphology of the spore-bearing organs. I do feel, however, that the course followed by that writer and by Hirmer lends excessive flexibility to the concept of *Asterotheca.*

Acknowledgment.—

The investigations reported here have been made possible chiefly through the generous cooperation of Mr. John E. Jones. I am deeply grateful for his continued support and enthusiastic interest in our studies. To the other employees of the Old Ben Coal Corporation who have extended aid I wish to extend sincere thanks.

My collecting trips to the Old Ben Mine have all been in company with Dr. James M. Schopf, now of the United States Bureau of Mines, and to him is due a very large share of the credit for such results as have been obtained thus far. The fine cuticle preparations illustrated on pl. 11, as well as the text-figure, were prepared by Dr. Schopf, and I am indebted to him for a considerable portion of the description of the sterile *Pecopteris* foliage. It should be noted, however, that the author assumes all responsibility for any of the theoretical views presented.

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Explanation of Plate

PLATE 10

Senftenbergia plumosa (Artis) Radforth var. *Jonesi* Andrews

Fig. 1. Photograph of the entire specimen; x 7.

Fig. 2. A portion of one of the pinnae magnified to show the abundance of sporangia; x 11.

Fig. 3. A portion of a pinnule showing the marginal position of the sporangia; x 20.

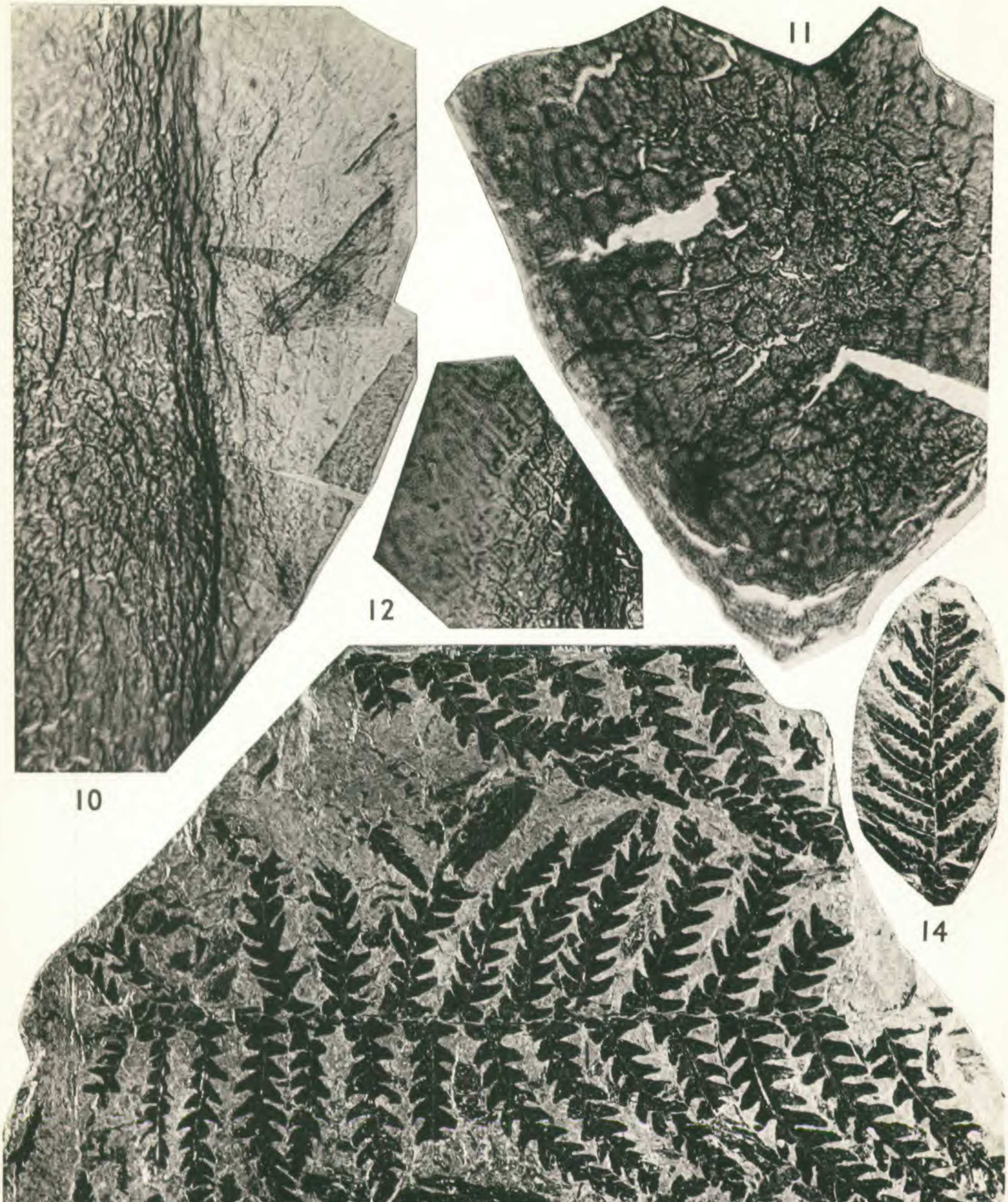
Figs. 4, 5. A single sporangium shown under different lighting conditions to bring out the cellular details of the wall; x 110 and x 80 respectively.

Fig. 6. A hair showing the characteristic septate structure; x 440.

Figs. 7, 8. Sporangial masses as they appear after partial oxidation of the sporangium wall; both x 150.

Fig. 9. A single mature spore; x 440.

ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VI



ANDREWS—AMERICAN CARBONIFEROUS FLORAS. VI

Explanation of Plate

PLATE 11

Pecopteris plumosa var. *dentata* (Bgt.) White

Fig. 10. Cuticle; central heavier band represents the leaf margin, the dorsal (lower surface) cuticle is adjoined on the right. x 140.

Fig. 11. Ventral cuticle from the area between the branches of a bifurcated lateral vein; x 140.

Fig. 12. Dorsal cuticle at leaf margin; marginal zone at the right; x 140.

Fig. 13. Portion of a frond showing the primary rachis at the left and parts of three secondary pinnae; natural size.

Fig. 14. Pinnule of more delicate structure; x. 7.

Explanation of Plate

PLATE 12

Senftenbergia plumosa var. *Jonesi*

Fig. 15. Portion of pinna rachis showing the epidermal hairs; x 6.
Fig. 16. Apical portion of a sporangium; x 95.
Fig. 17. Branching epidermal hairs; x 440.

Scolecopteris Radforthii

Fig. 18. Portion of an ultimate pinna showing venation of the pinnules; x 10.
Fig. 19. Lower surface of a pinnule showing the compressed synangia; x 20.